Amer. Malac. Bull. **27**: 83-93 (2009)

Documenting molluscan evolution from ancient long-lived lakes: The case of *Toxosoma* Conrad, 1874 (Gastropoda, Cochliopidae) in Miocene Amazonian Lake Pebas*

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Abstract: Long-lived lakes with their often *in situ* evolved faunas form an excellent model system to study evolution. The paleontological record of long-lived lakes provides possibilities to investigate the tempo and mode of evolutionary change. However, in order to demonstrate such processes, a combined rigorous temporal and spatial framework is needed in order to make sure (1) alleged evolutionarily successive morphs are not misidentified immigrant species and (2) morphological variation is not due to ecophenotypy. Other factors that may cause the development of discrete morphs, such as sexual dimorphism, also must be considered. In this paper, evolution in the Miocene snail genus *Toxosoma* Conrad, 1874 from long-lived Lake Pebas in western Amazonia is studied within such a temporal and paleo-environmental framework.

Key words: anagenesis, cladogenesis, temporal/spatial framework, gastropod evolution

Long-lived lakes are considered as laboratories and archives of evolution (Martens 1997). Faunas of these lakes, such as the well-known African cichlid fish, have served in many groundbreaking studies on adaptation, niche partitioning, sexual selection, and other mechanisms underlying the process of speciation. Molluscs (and ostracods) are abundant in these lakes and contain hard shells that have a good fossilization potential. Their fossils have frequently been used in exploring these archives of evolution (*e.g.*, Williamson 1981a, 1981b, Mensink 1984, Geary 1990, Geary *et al.* 2002, Harzhauser and Mandic 2004, Wesselingh 2007). However, evolutionary insights based on the fossil record of long-lived lakes have been diverse and partially contradictory. A well-known example is the debate on alleged punctuated evolutionary change in Kenyan Lake Turkana mollusc faunas as proposed by Williamson (1981a, 1981b) and hotly contested afterwards (see references in Bocxlaer *et al.* 2007). In several studies, morphological change in successive stratigraphic intervals has been taken as evidence for evolution, underestimating the potential role of ecosystem variability and intrinsic biological processes involved in the generation of morphological variation in molluscs.

In this paper we aim to demonstrate that the fossil record of long-lived lakes is very well suited for the study of evolutionary patterns as long as adequate account is taken of the spatial and temporal context. The study is based on stratigraphic successive morphological change in snails of the genus *Toxosoma* Conrad, 1874 (Rissooidea: Cochliopidae), in Amazonian Lake Pebas during the Middle and early Late Miocene. The methodological context by which evolution might be demonstrable is outlined.

LONG-LIVED LAKES

Long-lived lakes are lakes that combine geological longevity and the development of endemic faunas. Geological longevity is not strictly delimited but usually taken as being longer than an interglacial time interval. The current Lake Victoria in East Africa, with its more than thousand endemic cichlid fish species, was completely desiccated only about 13 ka ago (Johnson *et al.* 1996). However, Quaternary Lake Ioanina in northern Greece existed for at least several hundreds of thousands of years, yet almost completely lacked endemic species (Frogley and Preece 2007). In order to develop endemic faunas, a lake must have been habitable for some time. Thirteen thousand years is the shortest known long-lived lake. Although lakes may persist over long time periods, it is the temporal continuity of ecological conditions under which lacustrine biota can live that is the most important feature of long-lived lakes (Wesselingh 2007). Typically, ecological continuity is on the order of 100 ka to several Ma. The faunas in long-lived lakes contain a significant proportion of endemic species. These lakes often show high

* From the symposium "Molluscs as models in evolutionary biology: from local speciation to global radiation" presented at the World Congress of Malacology, held from 15 to 20 July 2007 in Antwerp, Belgium.

within-habitat diversity. The endemic species can be anagenetic derivatives of more widespread sister species (references in Wesselingh 2007), but in many of the long-lived lakes *in situ* radiations occur (Michel 1994, Müller *et al.* 1999, Nevesskaja *et al.* 2001, Geary *et al.* 2002). Such radiations have led to species flocks, *i.e.*, monophyletic clades of mostly or entirely endemic species (West and Michel 2000). Long-lived lake faunas have a broad range of morphologies, often containing marine-like features such as unusually thick and strongly ornamented shells and apertural modifications including siphonal canals. A general trait shared by endemic taxa in long-lived lakes is the tendency to evolve K-reproductive strategies (Michel 1994). An exception has been documented from Late Miocene lake Pannon of central-eastern Europe, where secondary opportunist, endemic bivalve species evolved as r-strategists (Harzhauser and Mandic 2004).

Long-lived lakes can be found in rift valleys (such as Lake Baikal in Russia and Lake Tanganyika in East Africa), in karst depressions (Lake Pozo in Indonesia and Lake Ohrid on the Balkans), in tectonic depressions (Lake Titicaca in South America and Lake Biwa in Japan), and even in meteorite craters (Miocene Lake Steinheim in southern Germany). They may be located at or below sea-level and contain brackish water such as the Caspian Sea and Neogene Paratethyan lakes of southeastern Europe. The oldest, long-lived lacustrine mollusc fauna known is that of the Permian South American Parana Lake (Wesselingh 2007). Lake Pebas, occupying western Amazonia during the Early to early Late Miocene (ca. 23-11 Ma), was located in the Andean foreland basins and adjacent pericratonic basins. At its maximum, the lake measured over 1 million km^2 in area (Wesselingh *et al.* 2002).

EVOLUTION AND THE FOSSIL RECORD

When working with fossils, species concepts are almost entirely morphologically based. Species can be defined by certain, unique combinations of ranges of morphological characters. However, (sexual) dimorphism is an inherent biological process known to produce distinct morphs within species. The possibility that different morphs may represent males and females must therefore be considered in evolutionary studies as well. Freshwater gastropod species are also well known to show ecophenotypic variation, *i.e.*, morphological variation related to habitat differences lacking a hereditary basis. Several mollusc groups exist whose species, as identified by DNA or ecological preferences, cannot be

Toxosoma contortum Wesselingh, 2006

Intermediate sized elongate to ovate-conical shell
Aperture flaring
Plane of aperture tilted backwards
Aperture contorted by well developed columellar plicae
Well developed teeth behind aperture within outerlip

Toxosoma grande Wesselingh, 2006

Large bulbous, comparatively thin shell
Convex whorl profile
Lacking teeth/spiral ridges inside outerlip
Columellar plicae absent or very low
Large and wide aperture

Toxosoma denticulatum Wesselingh, 2006

Intermediate-large ovate to ovate-conical shell
Thick shell
Suture very shallow
Whorl profile comparatively flat
Apertural margins reinforced
Columellar plicae very robuste
Well developed teeth behind aperture within outerlip
High aperture

Toxosoma eboreum Conrad, 1874

Intermediate sized ovate-conical shell
Thick shell
Somewhat deepened suture
Semiconvex whorl profile
Base bodywhorl slightly bulbous
Columellar plicae small but well developed
Teeth behind aperture within outerlip of variable strength

Figure 1. *Toxosoma* species from the Middle to early Late Miocene Pebas Formation of western Amazonia. Specimen and locality information in Wesselingh (2006). Scale bar = 1 mm.

distinguished on shell morphology, either by the lack of sufficient characters or by an abundance of apparently widely variable and overlapping characters. Within long-lived lakes taxa that are extremely difficult to separate based on shell characters are present, among others, Lake Tanganika snail species of the genus *Lavigeria* Bourguignat, 1888 (Michels 2004). However, detailed study of distribution patterns, ecology, and DNA may lead to grouping of specimens that turn out to have more or less subtle but distinctive morphological traits after all (Papadopoulos *et al.* 2004). Nevertheless, it can be expected that shell morphology cannot always be informative as to species discrimination. This may especially be the case in evolutionary transitional forms. The importance of sound systematics is not a trivial issue. Bocxlaer *et al.* (2007) showed that the erroneous generic identification of gastropod taxa in Lake Turkana has severely corrupted the evolutionary claims of Williamson (1981a, 1981b).

Evolution in fossil biotas can be defined as morphological change in lineages (anagenesis) and the origination of novel morphologies within clades (cladogenesis) through time in as far these cannot be ascribed to ecophenotypy or polymorphism. In order to demonstrate evolution, both control over stratigraphic time (temporal control) as well as the architecture of depositional environments is needed to address ecophenotypy (spatial control).

MATERIALS AND METHODS

Toxosoma eboreum Conrad, 1874 is the single *Toxosoma* species (Gastropoda, Cochliopidae) known from Middle Miocene intervals of the Pebas Formation (Wesselingh 2006). In successive late Middle to early Late Miocene intervals, three species are found (*Toxosoma denticulatum* Wesselingh, 2006; *Toxosoma contortum* Wesselingh, 2006; *Toxosoma grande* Wesselingh, 2006). The species have a range of shell characters that allow for their discrimination (Fig. 1).

Since *Toxosoma* is endemic to the Pebas system, it is possible that the latter three species originated from a single Middle Miocene ancestor (see Discussion section below). Together with a further three species found in earlier stratigraphic intervals in the Pebas Formation, *Toxosoma* may constitute a classical species flock. In the Pebas system, several putative species flocks occur, including a flock of the cochliopid genus *Sioliella* Haas, 1949. In order to assess whether the three species are not mere ecophenotypes or sexual dimorphs we have measured specimens from different stratigraphic and depositional environments. A total of 278 specimens belonging to the four species were retrieved from 17 Miocene Pebas Formation localities in Colombian and Peruvian Amazonia (Table 1, Fig. 2, Appendix 1). A single unidentified specimen was also included in the analyses.

Table 1. Localities; detailed information (including coordinates, collection dates, and maps) can be found in Wesselingh (2006) and Wesselingh *et al.* (2002, 2006b). MZ, mollusc zonation from Wesselingh *et al.* (2006b). ENZ, inferred environment from facies analyses (Räsänen *et al.* 1998, Wesselingh *et al.* 2006a) and from multivariate analysis of mollusc samples (Wesselingh *et al.* 2002). F, fluvial; ML, marginal lacustrine (prodelta, interdistributary bay, shoreface); L, lake shelf and bottom.

Sample	Locality	MZ	ENV
F4	Mocagua (Amazonas, Colombia)	10	ML
F6	Mocagua (Amazonas, Colombia)	10	ML
F16	Los Chorros I (Amazonas, Colombia)	10	F
F21	Los Chorros III (Amazonas, Colombia)	10	ML
F22	Los Chorros III (Amazonas, Colombia)	10	L
F29	Puerto Nariño I (Amazonas, Colombia)	11	ML-F
F32	Macedonia (Amazonas, Colombia)	11	ML
F34	Zaragoza (Amazonas, Colombia)	11	ML
F363	Iquitos Puerto GansoAzul (Loreto, Peru)	6	ML-L
F367a	Nuevo Horizonte III (Loreto, Peru)	9	L
F417	Pebas XIII (Loreto, Peru)	7	L
F489	Santa Elena I (Loreto, Peru)	8	ML
F498	Santa Elena II (Loreto, Peru)	8	L
F535	Santa Rosa de Pichana (Loreto, Peru)	7	L
F685	Tamshiyacu (Loreto, Peru)	7	ML
F702	Porvenir II (Loreto, Peru)	9	F
F707	Porvenir IV (Loreto, Peru)	9	L
F830	Momon III (Loreto, Peru)	7	L-ML
F836	Nuevo Horizonte II (Loreto, Peru)	9	L

The specimens were first identified using apertural outline and inclination, whorl profile, nature and number of columellar plicae, and grooves/denticles within the outer lip (Fig. 1). Three characters [height (H), height of aperture (Hap), and width of body whorl half a whorl before termination (WBW)] were measured with a resolution of 20 μm (Fig. 3). In *Toxosoma* specimens, the last quarter of the body whorl has a tendency to flare, which can be considered an adult apertural modification (Papadopoulos *et al.* 2004). The extent of flaring can vary considerably within and between populations. The maximum shell width (W) that is linked to the extent of flaring is too variable a measure and has been excluded from study. In many of the specimens, the aperture is damaged, precluding width measurements. In this study, the width of the shell half a whorl before the aperture is used in order to circumvent the above-mentioned problems. In three of the four species, the aperture tends to become tilted, making the height of the aperture (Hap) another potentially problematic character for study. However, we observed a remarkable correlation between W and

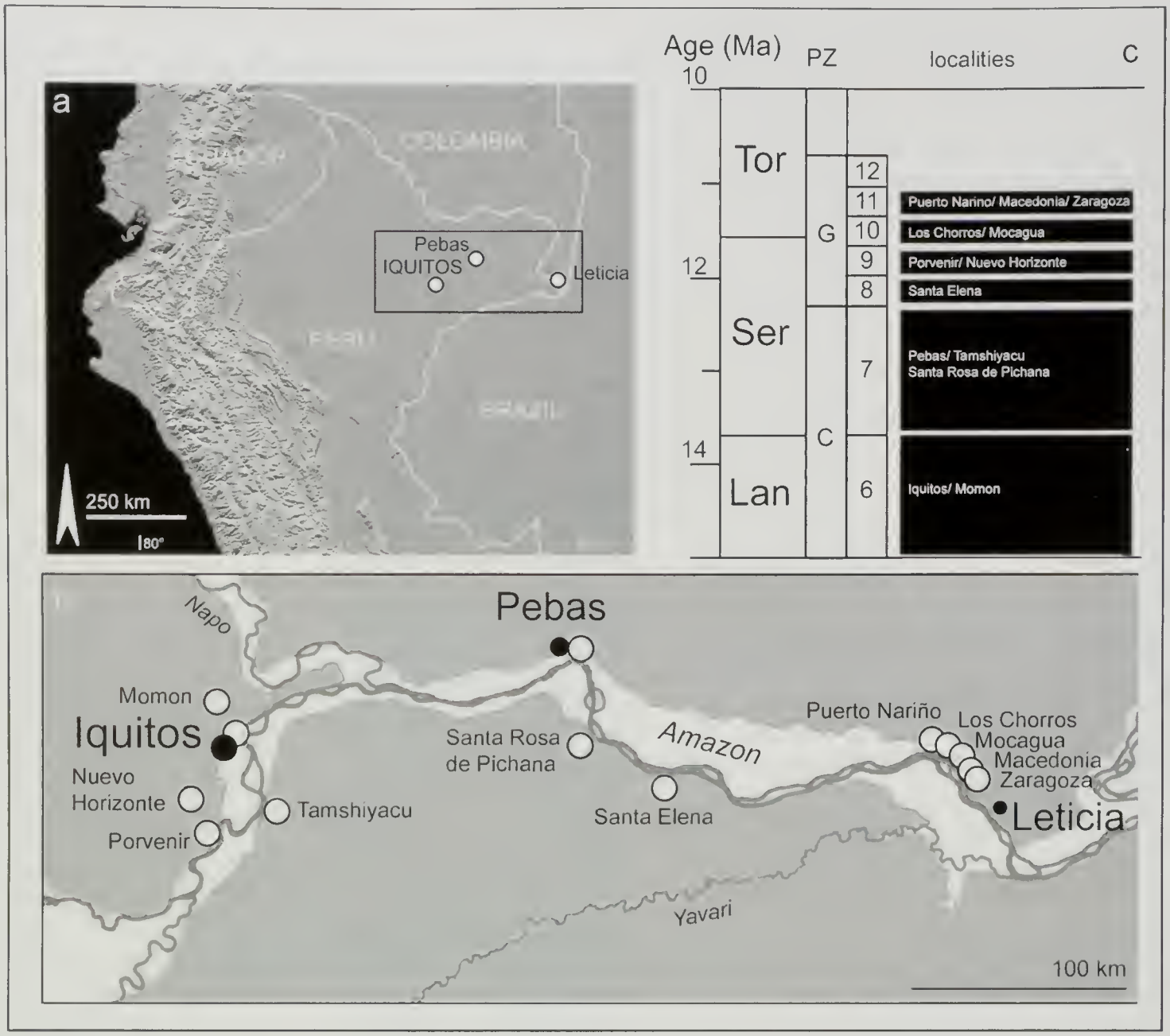

Figure 2. Localities and stratigraphic context of studied material. A, fieldwork area. B, localities: white areas denote alluvial plains, grey areas indicate uplands (so called "terra firme") that are underlain mostly by Neogene deposits. C, stratigraphic framework for the studied samples. Tor, Tortonian; Ser, Serravallian; Lan, Langhian; PZ, pollen zones (Hoorn 1993); G, *Grimsdalea* zone; C, *Crassoretitriletes* zone; numbers refer to mollusc zones from Wesselingh *et al.* (2006b).

Hap, strongly suggesting that the Hap is a usable character in spite of variations in the tilt of the apertural plane. Finally, the number of whorls was counted (Fig. 3).

A Principal Components Analysis (PCA) was performed on the variables H, Hap, WBW, and Wh (N = 276) with Primer 6.1 (Clarke and Warwick 2001). Width (W) was excluded because of the large number of missing measurements. The first two principal components were plotted in morphological space for each stratigraphical interval. The depositional environments of the *Toxosoma* species are inferred from sedimentary facies analyses (Räsänen *et al.* 1998, Wesselingh *et al.* 2006a) and from multivariate analysis of mollusc samples (Wesselingh *et al.* 2002). A variety of habitats, ranging from fluvial to lake bottoms, have been discerned.

RESULTS

In stratigraphic zones MZ6-MZ8, only the species *Toxosoma eboreum* is present. In samples from zones MZ9-MZ11, *T. contortum*, *T. grande*, and *T. denticulatum* co-occur. Within species, size differences were observed in different samples. All identifications apart from one (see Discussion below) were unambiguous.

Shell measurements are presented (Appendix 1). The first two principal components (PC1 and PC2) plotted here account for 97% of the variance in the data (per-axis inertia: PC1 = 0.85; PC2 = 0.12). PC1 represents mostly size parameters (H, Hap, WBW-1). The second PCA axis is strongly determined by the number of whorls. PC1 and PC2

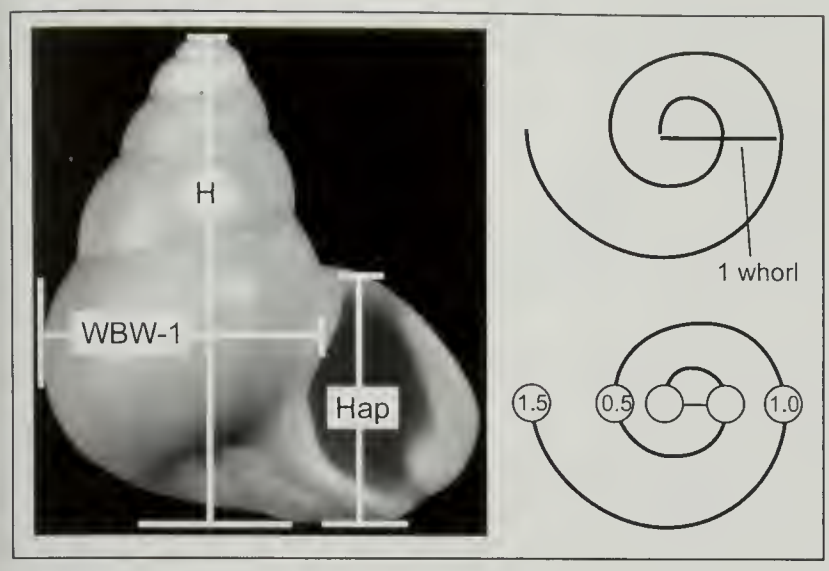

Figure 3. Characters measured. H, height; WBW-1, width of body whorl between half a whorl and one whorl before the termination of the shell; Hap, height of aperture. Whorls are counted as in upper right. The width per whorl is counted as in lower right.

scores are provided for the different species per stratigraphic interval (Fig. 4).

Toxosoma eboreum occurs in the lower three stratigraphic zones (MZ6-MZ8). The populations in the MZ6 samples have low PC1 scores and variability. PC1 scores and variability are larger in the overlying two stratigraphic zones. The populations in all three zones have intermediate PC2 scores.

In stratigraphic zones MZ9-MZ11, *Toxosoma contortum* is characterized by low PC1 scores and intermediate PC2 scores. In MZ9, PC1 scores are most variable and partially overlap those of *T. eboreum* in the underlying MZ8. In the overlying MZ10 and MZ11, the average PC1 score slightly increases.

In MZ9, *Toxosoma grande* and *T. denticulatum* have very similar PC1 scores, but are well distinguished by PC2 scores (low for *T. denticulatum* and high for *T. grande*). In the overlying MZ10 and MZ11, the PC2 values of both species largely overlap. A notable increase in PC1 values and variability is found for *T. grande* in successive stratigraphic zones.

The unidentified *Toxosoma* species from interval MZ10 scores between PC values of *T. contortum* and *T. grande* in that interval. In three of the four species (*Toxosoma eboreum*, *T. contorum*, *T. grande*) an increase in PC1 values in successive time intervals is observed and corresponds to an anagenetic increase in size.

DISCUSSION

The data indicate anagenetic change in *Toxosoma eboreum* in stratigraphic zones MZ6-MZ8. The apparent existence of two morphs within MZ7 is discussed below. It is possible that *T. eboreum* evolved from *T. ovatum* Wesselingh, 2006 that is common in MZ5.

The apparent (because of low number of samples) sudden occurrence in MZ9 of *Toxosoma contortum*, *T. denticulatum*, and *T. grande* is interpreted to result from cladogenesis (see below). More detailed sampling is required to establish the exact order of branching. The three species are well delimited through morphological characters as well as PC scores in MZ9 samples. However, the PC scores of the latter two species largely overlap in the upper two stratigraphic zones (MZ10 and MZ11). The PC1 values of both *T. contortum* and *T. grande* increase in successive intervals, again indicating anagenetic change towards larger sizes. On the scale of the mollusc biozones, both apparent "punctuated" (the occurrence of three species in MZ9) as well as gradual change (*e.g.*, directional change within *T. contortum*, *T. eboreum*, and *T. denticulatum* lineages) occurs. The exact time associated with the biozones is unknown but presumably on the order of several hundred thousand years per zone (Wesselingh *et al.* 2006a). The current sampling density and time control does not allow assessing whether the cladogenesis between MZ8 and MZ9 was sudden.

The unidentified specimen in MZ10 may be an aberrant specimen of one of the three species occurring in that zone. It also may represent a fifth species. However, we consider the last option unlikely as no similar specimens have been found in the large collection of Pebas material available. Finally, the unidentified morph may also represent a hybrid between *Toxosoma contortum* and *T. grande* or *T. denticulatum*. The limits imposed by the fossil record do not allow for an interpretation of the unidentified species.

Toxosoma eboreum lived in lacustrine and marginal lacustrine habitats (see Table 1; Wesselingh *et al.* 2002). *Toxosoma grande* is a species from marginal lake habitats (interdistributary bay, delta, and pro-delta) and fluvial habitats (see Table 1; Wesselingh *et al.* 2002). The lack of morphological intermediates with the other two co-occurring *Toxosoma* species in marginal lacustrine habitats indicates that they are not ecophenotypic morphs.

Toxosoma denticulatum inhabited lake margins and lake shelves although low numbers occur in samples from lake bottom settings that were not sampled in this study. *Toxosoma contortum* has a similar distribution although more common in lake bottom samples. Since both species occur in the same habitats (Table 1) and lack morphological intermediates, they too are unlikely to be ecophenotypic variants.

The three *Toxosoma* species occurring in MZ9-MZ11 have partially overlapping environmental optima. *Toxosoma grande* has its optimum in marginal lacustrine habitats, *T. denticulatum* on the lake shelf, and *T. contortum* on the lake shelf and lake bottom. A number of large samples containing

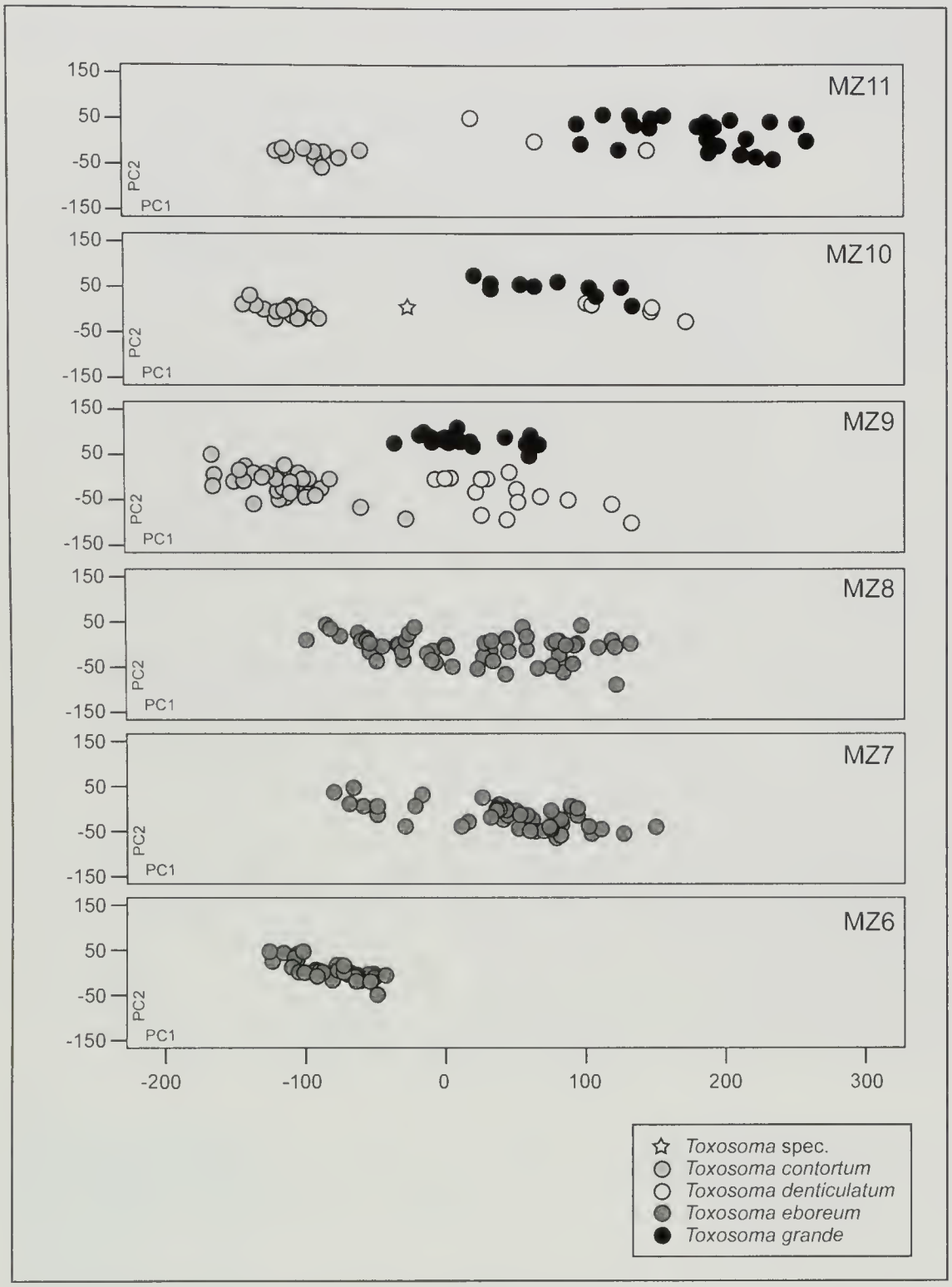

Figure 4. Character development in Pebasian *Toxosoma* species. MZ numbers refer to mollusc zones. PC1 and PC2 refer to the PCA axes.

solely *T. grande* suggest that the form is not simply a male or female sexual dimorph, as at least some of the specimens corresponding to the other sex would be expected. Various samples containing only *T. contortum* were found in stratigraphic zones and depositional environments where *T. denticulatum* also may have lived. This also indicates that it is unlikely that both forms are male and female morphs of a single species. Furthermore, in such a case a similar development in early ontogeny would be expected with divergence in adult stages (Shaver 1953). In some samples of *T. eboreum* and *T. denticulatum*, apparent slender and broad morphs co-occurred. Pronounced sexual dimorphism has been demonstrated to occur in some cochliopid gastropod species (Taylor 1987). Width/whorl measurements on both afore-mentioned *Toxosoma* species refute the presence of two well-delimited forms that might have represented sexual dimorphs (Fig. 5).

Documenting morphological change through time does not equate with documenting evolution. Other possible causes for morphological variability, such as ecophenotypy and sexual dimorphism, need to be accounted for. Furthermore, one needs to ascertain that the successive morphs are members of a single lineage. Endemic lineages in fossil long-lived lakes, such as the gastropod genus *Toxosoma* in Miocene Lake Pebas, comply with the latter assumption. The inferred cladogenetic event giving rise to three *Toxosoma* species in interval MZ9 may also have resulted from the invasion of species that developed elsewhere in the large (>1 million km^2) Pebas system. However, the morphological variability of closely related species is very low within stratigraphic intervals, even in samples from locations far apart (Wesselingh *et al.* 2006b). The geological record also provides opportunities to consider the potential role of environmental variation in generating morphological variation, and the shells themselves may provide clues about the possibility of dimorphism, making them a very suitable model to study speciation.

The three species whose distributional optima are in lacustrine habitats (*Toxosoma eboreum, T. denticulatum*, and *T. contortum*) developed thick shells with pronounced denticulation. The single marginal lacustrine-to-fluvial species (*T. grande*) has a comparatively thin shell, large aperture, and lacks well-developed denticles. The thick shells of the lacustrine species are possibly related to very abundant shell-cracking fish populations in the lake habitats. Teeth of sciaenid fish, a shell-cracking group, are often found in lacustrine samples from the Pebas Formation. A causal relationship is speculative at the moment. Scars of failed predatory attacks are common

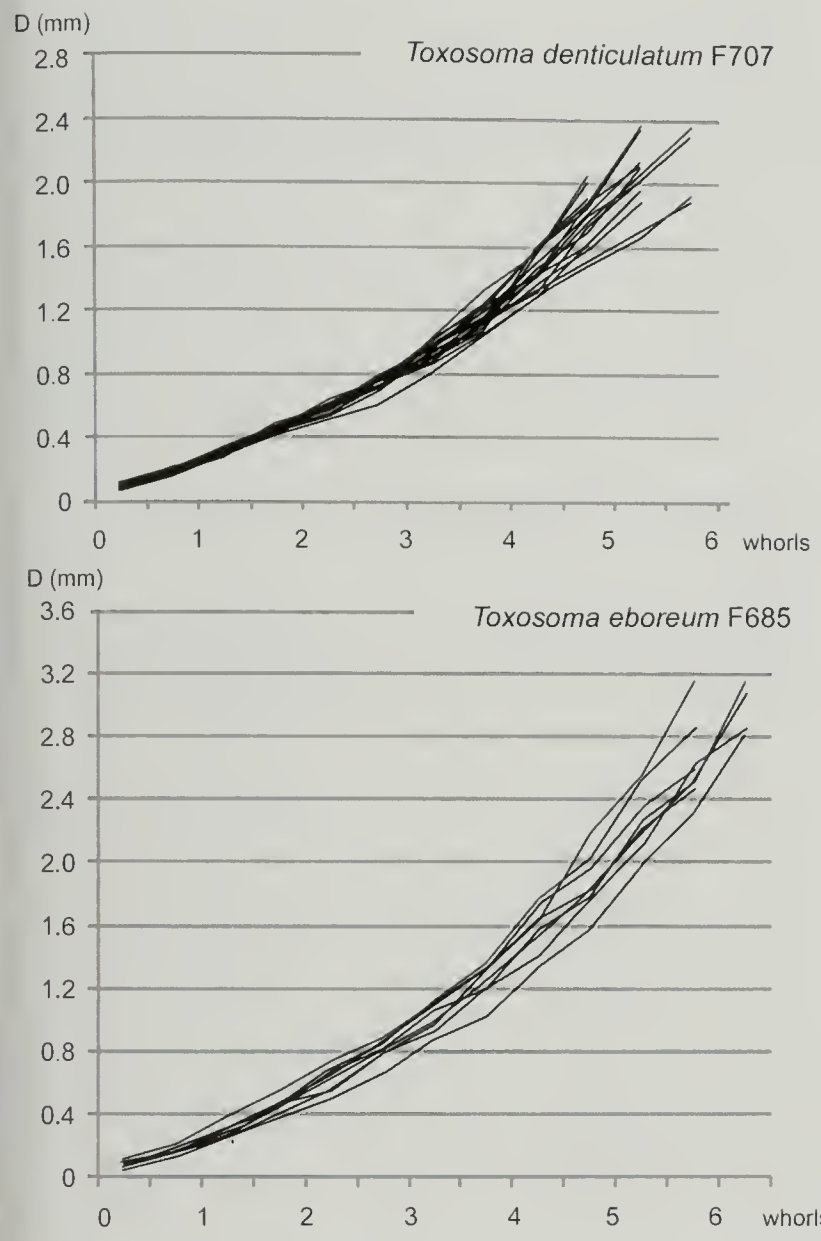

Figure 5. Width per half revolution (see Fig. 3 for explanation). *Toxosoma eboreum* and *T. denticulatum* have almost identical growth curves, the latter grows only to larger sizes and appears to develop two morphs that may represent sexual dimorphs in later stages of ontogeny. D, diameter. F707 and F685 refer to sample numbers (see Table 1).

on *Toxosoma* shells, however. In the lacustrine species such scars appear to match attacks from crushing predators (exemplified by the damage illustrated in Wesselingh 2007 on Pebasian *Pachydon obliquus* Gabb, 1869). The outer lip of *T. grande* is often damaged in a way that suggests the action of predatory crabs.

Geary (1990) studied morphological change within species of *Melanopsis* Ferussac, 1807 in the Late Miocene long-lived Lake Pannon in Austria and Hungary and found anagenetic change followed by a gradual cladogenetic split. The split probably developed over a time interval of approx. one million years and was accompanied by the shift of the two daughter species into different depositional environments. Geary's (1990) study is one of the very few documentations of gradual evolutionary change in long-lived lakes and shows that fossilized, long-lived lake shells provide great potential for such studies, as is corroborated with the *Toxosoma* study presented here.

CONCLUSIONS

In the case of the gastropod genus *Toxosoma,* an apparent cladogenetic event is documented in the Middle to early Late Miocene intervals of the Pebas Formation. The morphs correspond to species, and sexual dimorphism is found implausible as a possible cause for the observed morphologies.

ACKNOWLEDGMENTS

Matthias Glaubrecht and Thomas von Rintelen are thanked for organizing the symposium on "Molluscs as evolutionary models" at the World Malacological Congress in Antwerp (Belgium) in 2007 and for their invitation to contribute to this volume. We thank two anonymous reviewers for their comments. In particular, the thorough comments of one of the reviewers were of much help when considering data quality and interpretation as well as the language of an earlier version of this manuscript.

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Submitted: 9 April 2009; **accepted:** 13 April 2009;
final revisions received: 9 June 2009

Appendix 1. Measurements of *Toxosoma*. H, height; Hap, height of aperture; WH, number of whorls *100; WBW, width of shell half a whorl before termination (see Fig. 3).

Sample	Species	H	Hap	WH	WBW
F685	*T. eboreum*	510	260	610	285
F685	*T. eboreum*	460	220	580	265
F685	*T. eboreum*	465	260	550	275
F685	*T. eboreum*	470	240	590	275
F685	*T. eboreum*	440	220	550	255
F685	*T. eboreum*	445	210	580	255
F685	*T. eboreum*	465	230	605	265
F685	*T. eboreum*	485	230	570	285
F685	*T. eboreum*	480	230	605	260
F685	*T. eboreum*	450	215	560	260
F685	*T. eboreum*	495	240	610	280
F685	*T. eboreum*	445	220	570	250
F685	*T. eboreum*	525	275	595	295
F685	*T. eboreum*	475	240	555	290
F685	*T. eboreum*	440	215	545	250
F685	*T. eboreum*	475	230	580	275
F685	*T. eboreum*	430	210	530	245
F685	*T. eboreum*	465	240	560	265
F685	*T. eboreum*	480	220	620	270
F685	*T. eboreum*	475	230	615	275
F685	*T. eboreum*	450	225	600	255
F685	*T. eboreum*	435	230	560	255
F685	*T. eboreum*	500	250	600	275
F685	*T. eboreum*	455	230	605	260
F685	*T. eboreum*	475	220	600	270
F685	*T. eboreum*	485	250	595	280
F685	*T. eboreum*	470	230	595	265
F707	*T. contortum*	285	135	505	140
F707	*T. contortum*	335	150	600	160
F707	*T. contortum*	285	140	550	140
F707	*T. contortum*	340	135	600	155
F707	*T. contortum*	310	175	530	170

Appendix 1. (Continued)

Sample	Species	H	Hap	WH	WBW
F707	*T. contortum*	290	130	575	140
F707	*T. contortum*	355	150	580	180
F707	*T. contortum*	325	150	605	165
F707	*T. contortum*	380	165	620	185
F707	*T. contortum*	300	130	565	155
F707	*T. contortum*	305	140	550	155
F707	*T. contortum*	345	160	590	170
F707	*T. contortum*	320	155	560	165
F707	*T. contortum*	305	140	530	155
F707	*T. contortum*	315	145	550	160
F029	*T. grande*	555	295	520	290
F029	*T. grande*	535	335	515	295
F029	*T. grande*	520	265	495	275
F029	*T. grande*	595	295	510	340
F029	*T. grande*	610	310	515	340
F029	*T. grande*	575	310	550	320
F029	*T. grande*	550	320	510	325
F029	*T. grande*	515	275	500	325
F029	*T. grande*	505	275	520	295
F029	*T. grande*	515	290	505	290
F032	*T. grande*	485	250	515	265
F032	*T. grande*	580	335	590	300
F032	*T. grande*	560	290	580	305
F032	*T. grande*	500	290	575	265
F032	*T. grande*	590	325	595	320
F032	*T. grande*	560	315	565	295
F032	*T. grande*	550	310	525	295
F032	*T. grande*	520	295	525	275
F032	*T. grande*	550	310	550	300
F032	*T. grande*	575	320	585	300
F032	*T. grande*	600	350	555	330
F032	*T. grande*	495	265	495	275
F032	*T. grande*	550	310	525	310
F032	*T. grande*	495	245	560	260
F032	*T. contortum*	375	170	575	190
F032	*T. contortum*	350	160	580	185
F032	*T. contortum*	370	125	590	175
F032	*T. contortum*	380	140	590	180
F032	*T. contortum*	380	120	610	175
F032	*T. contortum*	350	125	585	165
F032	*T. contortum*	340	115	575	175
F032	*T. contortum*	375	115	575	175
F032	*T. contortum*	350	140	570	175
F032	*T. contortum*	340	135	570	165
F417	*T. eboreum*	455	230	570	255
F417	*T. eboreum*	435	215	555	255
F535	*T. eboreum*	425	240	560	250
F535	*T. eboreum*	360	185	550	200
F535	*T. eboreum*	420	215	585	235
F535	*T. eboreum*	390	195	525	230
F535	*T. eboreum*	355	175	545	195

Appendix 1. (Continued)

Sample	Species	H	Hap	WH	WBW
F535	*T. eboreum*	370	185	570	205
F535	*T. eboreum*	445	240	570	250
F535	*T. eboreum*	420	205	595	235
F535	*T. eboreum*	370	180	550	210
F535	*T. eboreum*	340	175	520	195
F535	*T. eboreum*	435	230	560	240
F535	*T. eboreum*	435	215	575	245
F535	*T. eboreum*	390	190	550	225
F535	*T. eboreum*	350	185	510	200
F535	*T. eboreum*	390	180	595	220
F836	*T. denticulatum*	520	290	655	250
F836	*T. denticulatum*	400	240	560	215
F836	*T. denticulatum*	445	245	650	225
F836	*T. denticulatum*	435	245	545	245
F836	*T. denticulatum*	410	210	560	205
F836	*T. denticulatum*	430	230	560	235
F836	*T. denticulatum*	400	235	560	210
F836	*T. denticulatum*	430	235	640	220
F836	*T. denticulatum*	470	205	580	240
F367	*T. denticulatum*	485	260	605	240
F367	*T. denticulatum*	505	280	615	255
F367	*T. denticulatum*	455	250	610	220
F367	*T. denticulatum*	415	255	590	215
F367	*T. denticulatum*	455	255	600	250
F367	*T. denticulatum*	430	240	560	215
F367	*T. contortum*	330	170	545	165
F367	*T. contortum*	340	160	560	175
F367	*T. contortum*	340	160	600	170
F367	*T. contortum*	310	150	545	150
F367	*T. contortum*	325	145	550	160
F367	*T. contortum*	330	140	585	165
F367	*T. contortum*	410	180	645	190
F367	*T. contortum*	325	160	580	160
F367	*T. contortum*	340	145	580	165
F367	*T. contortum*	310	145	615	155
F367	*T. contortum*	300	150	565	150
F367	*T. contortum*	325	150	560	160
F367	*T. contortum*	350	175	560	175
F367	*T. contortum*	315	145	545	165
F367	*T. contortum*	335	160	560	175
F367	*T. contortum*	335	150	565	165
F367	*T. contortum*	350	155	595	175
F367	*T. contortum*	335	155	590	160
F367	*T. contortum*	315	145	555	160
F367	*T. contortum*	300	140	540	155
F034	*T. denticulatum*	460	255	555	235
F034	*T. denticulatum*	520	295	575	270
F034	*T. denticulatum*	415	220	505	245
F498	*T. eboreum*	415	205	605	230
F498	*T. eboreum*	405	200	570	220
F498	*T. eboreum*	355	180	530	205

Appendix 1. (Continued)

Sample	Species	H	Hap	WH	WBW
F498	*T. eboreum*	390	185	555	205
F498	*T. eboreum*	405	195	575	215
F498	*T. eboreum*	385	170	570	185
F498	*T. eboreum*	410	200	595	215
F498	*T. eboreum*	435	220	570	240
F498	*T. eboreum*	460	200	620	245
F498	*T. eboreum*	395	170	590	180
F498	*T. eboreum*	350	165	510	180
F498	*T. eboreum*	400	180	555	195
F498	*T. eboreum*	420	230	585	245
F498	*T. eboreum*	430	220	610	230
F498	*T. eboreum*	370	175	540	200
F498	*T. eboreum*	380	195	590	220
F498	*T. eboreum*	380	160	545	190
F498	*T. eboreum*	370	170	545	205
F498	*T. eboreum*	375	190	560	200
F498	*T. eboreum*	405	200	560	240
F498	*T. eboreum*	410	195	590	215
F498	*T. eboreum*	340	150	545	180
F498	*T. eboreum*	400	190	570	190
F498	*T. eboreum*	360	170	535	180
F498	*T. eboreum*	385	165	550	190
F498	*T. eboreum*	350	170	520	180
F489	*T. eboreum*	490	235	615	250
F489	*T. eboreum*	395	185	545	210
F489	*T. eboreum*	455	200	540	255
F489	*T. eboreum*	445	210	550	225
F489	*T. eboreum*	470	210	565	250
F489	*T. eboreum*	420	195	555	220
F489	*T. eboreum*	495	215	575	255
F489	*T. eboreum*	500	220	550	270
F489	*T. eboreum*	460	215	515	255
F489	*T. eboreum*	500	220	510	275
F489	*T. eboreum*	470	205	535	255
F489	*T. eboreum*	535	230	640	265
F489	*T. eboreum*	475	230	550	260
F489	*T. eboreum*	505	245	545	290
F489	*T. eboreum*	485	225	545	260
F489	*T. eboreum*	495	210	600	250
F489	*T. eboreum*	400	180	530	210
F489	*T. eboreum*	500	220	555	265
F489	*T. eboreum*	480	220	545	270
F489	*T. eboreum*	495	210	555	270
F489	*T. eboreum*	525	240	550	290
F489	*T. eboreum*	405	190	515	200
F489	*T. eboreum*	435	180	560	215
F489	*T. eboreum*	460	190	590	235
F489	*T. eboreum*	510	250	560	280
F489	*T. eboreum*	505	220	595	255
F489	*T. eboreum*	450	205	545	235
F489	*T. eboreum*	510	225	560	280

Appendix 1. (Continued)

Sample	Species	H	Hap	WH	WBW
F489	*T. eboreum*	460	200	570	250
F489	*T. eboreum*	485	205	605	250
F022	*T. contortum*	345	140	545	160
F022	*T. contortum*	350	150	565	175
F022	*T. contortum*	335	155	570	165
F022	*T. contortum*	340	150	550	180
F022	*T. contortum*	345	150	575	165
F022	*T. contortum*	350	150	575	155
F022	*T. contortum*	350	165	575	170
F022	*T. contortum*	335	135	575	160
F022	*T. contortum*	335	150	550	165
F022	*T. contortum*	320	135	555	165
F022	*T. contortum*	330	135	560	170
F022	*T. contortum*	315	145	545	150
F022	*T. contortum*	300	145	545	155
F022	*T. contortum*	300	155	525	155
F022	*T. contortum*	330	155	555	160
F004	*T. grande*	460	255	495	270
F004	*T. grande*	515	280	545	270
F004	*T. grande*	420	245	500	240
F004	*T. grande*	450	250	505	255
F004	*T. grande*	445	240	500	250
F702	*T. grande*	420	210	465	220
F702	*T. grande*	475	220	480	250
F702	*T. grande*	430	180	465	220
F702	*T. grande*	435	195	475	235
F702	*T. grande*	460	240	480	235
F702	*T. grande*	400	195	460	215
F702	*T. grande*	415	180	465	220
F702	*T. grande*	405	190	455	215
F702	*T. grande*	425	205	475	225
F702	*T. grande*	415	200	475	225
F702	*T. grande*	380	185	480	215
F702	*T. grande*	450	225	465	235
F702	*T. grande*	435	205	485	230
F702	*T. grande*	405	185	460	215
F702	*T. grande*	405	220	480	225
F702	*T. grande*	470	215	505	250
F702	*T. grande*	420	185	475	210
F702	*T. grande*	470	220	460	245
F702	*T. grande*	420	195	445	240
F363	*T. eboreum*	360	180	560	220
F363	*T. eboreum*	370	160	560	215
F363	*T. eboreum*	335	175	550	210
F363	*T. eboreum*	340	170	540	205
F363	*T. eboreum*	360	180	575	200
F363	*T. eboreum*	330	165	550	195
F363	*T. eboreum*	325	150	525	190
F363	*T. eboreum*	315	170	515	185
F363	*T. eboreum*	360	180	560	180
F363	*T. eboreum*	355	165	560	175

Appendix 1. (Continued)

Sample	Species	H	Hap	WH	WBW
F363	*T. eboreum*	385	190	565	170
F363	*T. eboreum*	320	145	530	165
F363	*T. eboreum*	370	160	570	160
F363	*T. eboreum*	330	155	510	155
F363	*T. eboreum*	340	160	520	150
F006	*T. denticulatum*	550	290	580	285
F006	*T. denticulatum*	520	280	560	290
F006	*T. denticulatum*	490	260	540	260
F006	*T. denticulatum*	525	280	550	285
F006	*T. denticulatum*	485	270	545	265
F016	*T. grande*	430	220	510	250
F016	*T. grande*	495	245	505	270
F016	*T.* spec.	390	205	550	200
F016	*T. grande*	490	265	525	270
F016	*T. grande*	505	260	505	290
F021	*T. grande*	420	220	480	240
F830	*T. eboreum*	345	160	550	180
F830	*T. eboreum*	355	160	555	205
F830	*T. eboreum*	335	160	555	190
F830	*T. eboreum*	345	160	560	180
F830	*T. eboreum*	320	165	510	190
F830	*T. eboreum*	320	160	545	180
F830	*T. eboreum*	360	165	555	200
F830	*T. eboreum*	365	170	560	195
F830	*T. eboreum*	340	160	555	190
F830	*T. eboreum*	350	155	550	180
F830	*T. eboreum*	340	160	555	195
F830	*T. eboreum*	355	160	550	195
F830	*T. eboreum*	365	160	565	205
F830	*T. eboreum*	390	170	560	200
F830	*T. eboreum*	350	170	555	200
F830	*T. eboreum*	330	155	555	180
F830	*T. eboreum*	335	155	555	180
F830	*T. eboreum*	365	170	575	195
F830	*T. eboreum*	375	175	575	195
F830	*T. eboreum*	380	170	605	205
F830	*T. eboreum*	340	160	565	185
F830	*T. eboreum*	305	145	510	185
F830	*T. eboreum*	350	175	540	195